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OXYCHILUS (DROUETIA) AGOSTINHOI NEW SPECIES (STYLOMMATOPHORA: ZONITIDAE) FROM THE AZORES ISLANDS, ITS ANATOMY AND PHYLOGENETIC RELATIONSHIPS

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ABSTRACT. *Oxychilus (Drouetia) agostinhoi* n. sp. (Stylommatophora, Zonitidae) from Santa Maria, Azores, shares some characteristics with the subgenus *Ortizius* Forcart, but is placed in the subgenus *Drouetia* Gude on the basis of conchological and penial characters. The phylogeny of those species of *Oxychilus* Fitzinger endemic to the Azores supports the hypothesis of Riedel (1964) that the subgenera *Ortizius* and *Drouetia* evolved in the Azores from a pre-*Ortizius* type of mollusk which arrived from Europe, probably during the Tertiary. Based only upon its resemblances to Azorean species of the subgenera *Drouetia* and *Ortizius*, for which there is no fossil record, this new species is seen as having separated from the branch leading to *Oxychilus (Drouetia) atlanticus* s. l. before the origin of the subgenus *Atlantoxychilus* Riedel.

INTRODUCTION

The first significant publication on the land Mollusca of the Azores was by Morelet and Drouet (1857) which was revised and expanded by Morelet in 1860. Nobre visited the islands in 1919 and published two papers on the fauna in 1924 and 1930. Zonitid material was collected during the 1957 Swedish Zoological Expedition under the direction of P. Brink and E. Dahl and was described by Riedel in 1964. Backhuys (1975) gave a thorough analysis of the land mollusks collected in 1969 by the team integrated in the Inter-

national Project for the Investigation of the Macaronesian Area, relying on Riedel (1964) when dealing with the Zonitidae.

Collections are still not sufficient for a complete understanding of the distribution and relationships of Azorean mollusks either within or outside the archipelago. The purposes of this paper are to describe a new species of *Oxychilus* and to discuss the relationships and evolution of the endemic subgenus *Drouetia* Gude, particularly its affinities with the subgenus *Ortizius* Forcart. The results support the hypothesis of Riedel (1964) that both groups arose in the Azores from a pre-*Ortizius* type snail which had arrived from Europe, probably during the Tertiary.

The nine islands comprising the Azorean archipelago (Plate 28, fig. 1) lie on the mid-Atlantic ridge, 1450 km west of Portugal and 1776 km east-south-east of Newfoundland. Santa Maria Island (Plate 28, fig. 2) has an area of 97 km² and its highest point is only 580 m above sea level. It has ten endemic species and subspecies of land snails, the largest number of any of the islands. São Miguel Island, 80 km north and eight times larger, has only five endemic

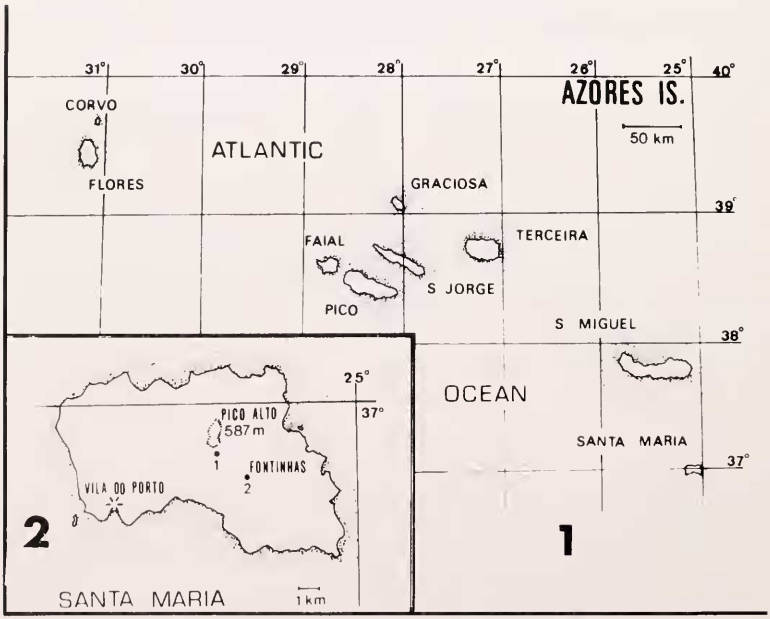

Plate 28

Fig. 1. Map of the Azores Islands.

Fig. 2. Map of Santa Maria Island, showing the collecting stations.

species. It is possible that, after a thorough study of the geological and biological history of the Azores, Santa Maria Island will prove to occupy a key position in the colonization of the archipelago.

ACKNOWLEDGMENTS

I wish to express my gratitude to Drs. Ruth D. Turner and Kenneth J. Boss of Harvard University and Dr. Robert C. Bullock of the University of Rhode Island for their continued assistance and comments on the manuscript.

MATERIALS AND METHODS

Specimens for anatomical work were killed by drowning in freshwater overnight and then preserved in 70% ethanol. No histological preparations or studies were made.

Specimens for examination with the Scanning Electron Microscope (SEM) were first cleaned in distilled water and then in 70% and 90% ethanol, using an ultrasonic cleaner for 10 seconds at each step. They were then mounted on a stub using double coated tape. Radulae were first cleaned in KOH, washed in distilled water and then carried to absolute ethanol to harden the teeth. To avoid destruction of the teeth, ultrasonic cleaning was reduced to two seconds per step. The radula ribbon was mounted on a circular cover glass to which it adhered when dry and the cover slip was attached to the stub with double coated tape. All specimens were covered with carbon and gold-palladium in a Denton DV-502 vacuum evaporator and examined using a ISI Mini-SEM, located in the Department of Zoology, University of Rhode Island.

Systematic work was based on the studies of Wollaston (1878), Gude (1911), Forcart (1957), Zilch (1959) and Riedel (1957, 1964, 1966). Terminology generally follows that of Fretter and Graham (1962) for the description of the soft parts, Rigby (1963) for the digestive and reproductive systems and Simroth (1908), Bargmann (1930) and Franc (1968) for the nervous system.

STATION DATA

Santa Maria Island, Azores Islands: *Station 1*, Pico Alto, south slope, at 500 m. In primitive forest of *Pittosporum undulatum* Vent, *Erica azorica* Hochst, *Laurus azoricus* (Seub) and the introduced *Hedychium gardnerianum* Roscoe. The animals had a special preference for fallen leaves of *Hedychium*. a. 1-XI-1974, 1 dead specimen; b. 9-X-1975, 1 dead and 7 live specimens.

Station 2. Fontinhas, Perímetro Florestal, at 300–400 m of altitude in forest of *Cryptomeria japonica* Don and *Myrica faya* Ait with an undergrowth of *Hedychium*. a. 1-XI-1974, 1 live and 1 dead specimen; b. 10-X-1975, 10 live and 8 dead specimens.

SYSTEMATICS

Family ZONITIDAE Mörch 1864

Subfamily ZONITINAE Mörch 1864

Genus *Oxychilus* Fitzinger 1833

Oxychilus Fitzinger 1833, Beträge Landesk. Oesterreich's unter der Enns [in] Verein fuer Vaterlaendische Geschichte . . ., [Vienna] 3 (3): 100. Type species, *Helix cellaria* Müller, subsequent designation Herrmannsen 1847.

Shell thin, translucent, smooth, somewhat glossy, disc-shaped, moderately umbilicate to non-umbilicate; whorls about 6; sutures not impressed; axial striae indistinct; last whorl elliptical in profile; aperture oblique, lip simple, sharp.

Subgenus *Drouetia* Gude 1911

Drouetia Gude 1911, Proc. Malacological Soc. London *9*:272. Type species, *Helix atlantica* Morelet and Drouet, original designation.

Foot tripartite, right posterior tentacle retractor crossing the reproductive organs. Shell imperforate, hyaline, shiny, smooth, sculpture (at 400×) of extremely fine spiral lines crossed by axial threads.

Oxychilus (Drouetia) agostinhoi, new species[1]

Plates 29–35

Type Locality. Fontinhas, Perímetro Florestal, 300–400 m, Santa Maria Island, Azores Islands.

Type Repositories. Holotype and two paratypes, Museum of Comparative Zoology, nos. 288926, 288927, 288928. Additional paratypes at the American Museum of Natural History (1 sp.) Academy of Natural Sciences, Philadelphia (1 sp.), National Museum of Natural History, Washington, D.C. (1 sp.), British Museum (Natural History), London (2 sp.), Musée d'Histoire

[1]By naming this species after the late Ten.-Cor. José Agostinho, I express my deepest homage to an eminent Azorean scientist and a very dear friend.

Naturelle, Paris (1 sp.), Musée d'Histoire Naturelle "Gr. Antipa", Bucharest (1 sp.), and collection of the author.

Description. Shell (Plate 30, Plate 31, figs. 5–6). Shell dextral, small, reaching 5.1 mm in maximum diameter, disc-shaped, non-umbilicate, whorls 4–4¼, horn-colored or somewhat greenish, with a greasy shine, transparent to translucent, apparently smooth, thin, fragile; first whorls whitish; position of old peristomes persisting as irregularly spaced light and dark axial bands; last whorl elliptic in profile; aperture oblique, depressed; peristome simple, sharp, not continuous; parietal callus whitish, covering the umbilical region where it forms a cup-like depression (Plate 31, fig. 5); suture very shallow; growth lines irregular and very weak; high magnification reveals the presence of very fine regular spirals (Plate 31, fig. 6). Measurements of the holotype and adult or nearly adult paratypes (with 4 whorls or more) are given in Table 1.

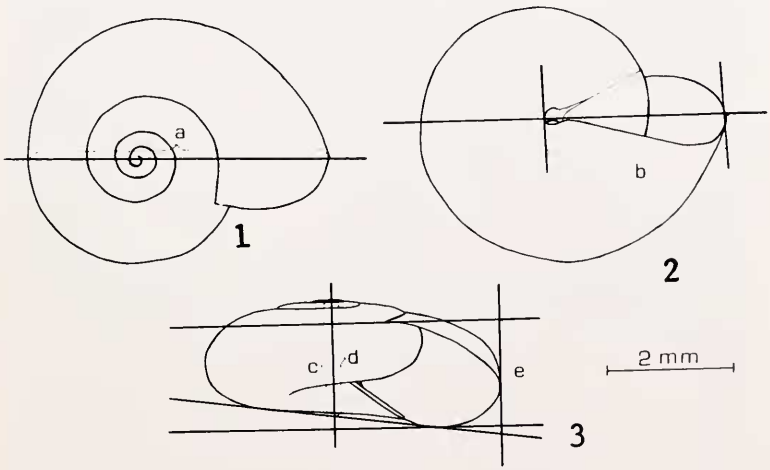

Plate 29

Figs. 1–3. Outline of the holotype, *Oxychilus (Drouetia) agostinhoi*, showing how the different measurements were taken. a, maximum diameter; b, aperture width; c. vertical height; d. oblique height; e, aperture height.

Animal. Neck dark-blue or brownish, becoming gradually lighter toward the foot and with a ring of more intense hue just above sole of foot; anterior tentacles small, grayish; posterior tentacles moderately long, black, their retractor muscles visible through skin; foot tripartite, a uniform light-gray to white; mantle with small, unevenly distributed patches of dark pigment mainly over dorsal region, visible only through the ventral surface of the

shell; mantle border black; genital opening marked by a whitish hue behind posterior right tentacle, about midway on neck.

Table 1. Measurements of the shells of the holotype (#315) and adult or nearly adult paratypes of *Oxychilus (Drouetia) agostinhoi*. Measurements in mm. The specimen number refers to my own collection. The mean is given as $\bar{X} \pm$ one standard deviation. For locality see text. For measurements see Plate 29, figs. 1–3.

Specimen number	Locality	Maximum diameter	Oblique height	Vertical height	Aperture height	Aperture width	Number of whorls
315	2b	5.1	2.0	2.2	1.8	3.0	4¼
506	2b	5.0	2.0	2.2	1.8	3.0	4
504	2b	5.0	1.9	2.2	1.8	3.0	4
505	2b	4.9	1.9	2.1	1.7	2.9	4¼
174	2a	4.9	2.1	2.4	1.9	3.0	4
377	1b	4.9	2.1	2.3	1.9	2.9	4
514	2b	4.9	2.0	2.4	1.8	2.6	4
507	2b	4.8	2.0	2.2	1.7	2.8	4¼
503	1b	4.8	1.9	2.1	1.7	2.8	4¼
508	2b	4.7	1.9	2.0	1.6	2.9	4
511	1b	4.6	1.9	2.3	1.8	2.9	4
313	2b	4.6	1.9	2.1	1.8	2.7	4
509	1b	4.6	1.9	2.1	1.8	2.6	4
515	2b	4.6	2.0	2.2	1.7	2.5	4
314	1b	4.5	1.7	1.9	1.5	2.7	4
510	1b	4.3	1.8	2.0	1.7	2.6	4
312	2b	4.2	1.9	2.1	1.8	2.4	4
Mean		4.7±.2	1.8±.1	2.2±.1	1.8±.1	2.6±.5	

Radula. (Plate 31, figs. 1–3. Plate 32). Radula formula:

$$\left[\frac{(12-13)}{1-(2)} + \frac{2}{3} + \frac{1}{3} + \frac{2}{3} + \frac{(12-13)}{(2)-1}\right] \times 42-55$$

Central tooth shorter and narrower than laterals, tricuspid; cusps about same size, small; central cusp always thinner than laterals. First lateral higher than central, tricuspid; inner cusp small, broad; median cusp long; outer cusp smaller than inner cusp, somewhat narrower. Second lateral similar to the first lateral, larger. Marginals falciform; first marginal bicuspid, with inner cusp rudimentary and outer cusp strong, curved; other marginals unicuspid, similar to the first marginal, becoming smaller.

Anatomy (Plate 33): *Organs of the neck region.* Anterior tentacles with grayish to dark gray internal wall; a thin contractor

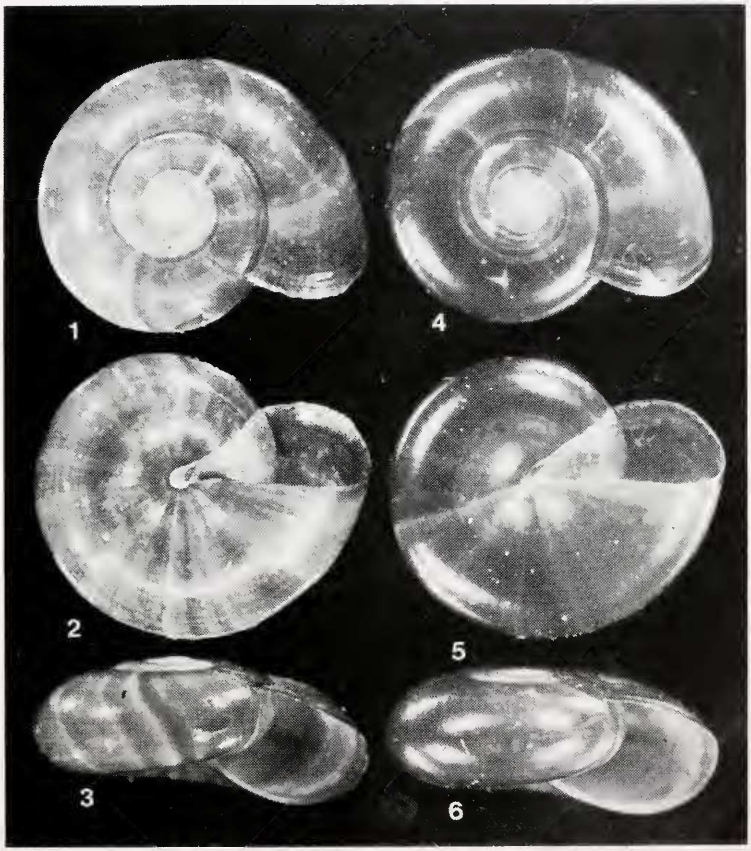

Plate 30

Figs. 1–6. *Oxychilus (Drouetia) agostinhoi*. Shell. Figs. 1–3, holotype (MCZ 288926) (5.1 mm max. diameter); Figs. 4–6, paratype (MCZ 288928) (4.5 max. diameter).

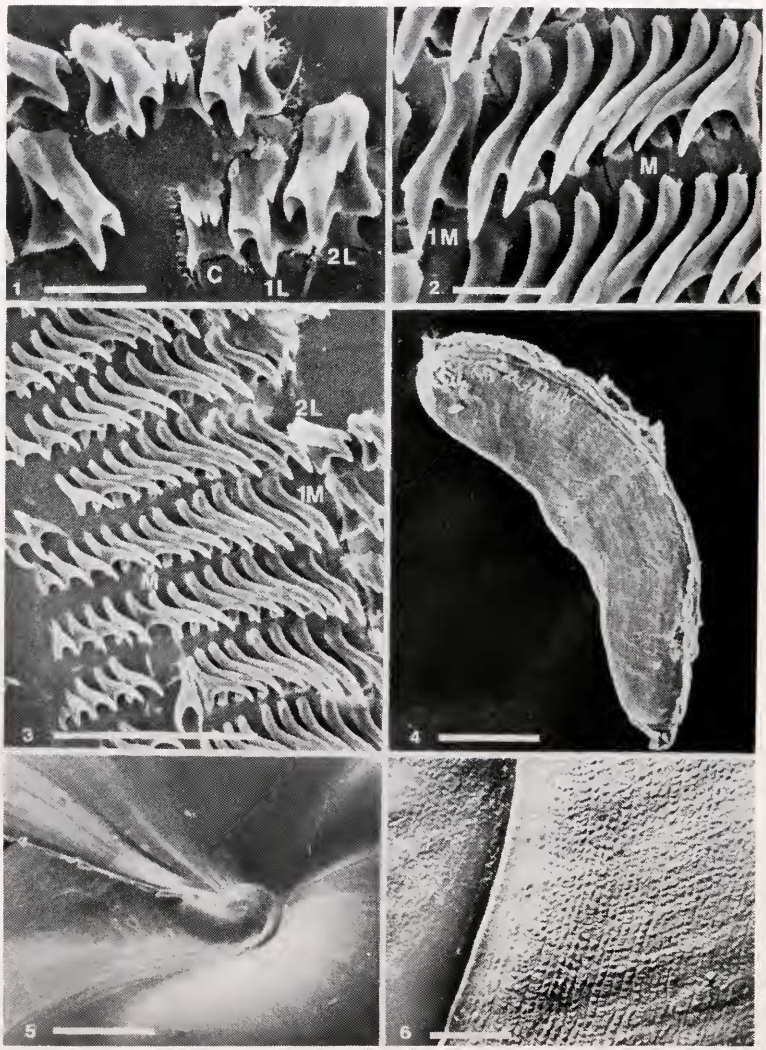

Plate 31

muscle arises near the attachment of the tentacle retractor muscle and inserts on the side of the foot; the retractor muscle adheres laterally to the cerebral ganglion and to most of the length of median lip nerve; the retractor muscle unites with the posterior tentacle retractor after receiving a nerve coming from the base of the pleural-pedal connective. Posterior tentacles bluish-black; two thin contractor muscles originate a little anterior to the insertion of the ocular nerve and attach at the base of each tentacle; right posterior tentacle retractor longer than the left, crossing the genital organs between penis and vagina. Two pairs of mucous glands dorsal to the foot open into the space between the lower lip and foot; the lower glands adhere posteriorly to the pedal ganglia, and are bordered laterally by the inner anterior pedal nerves, from which

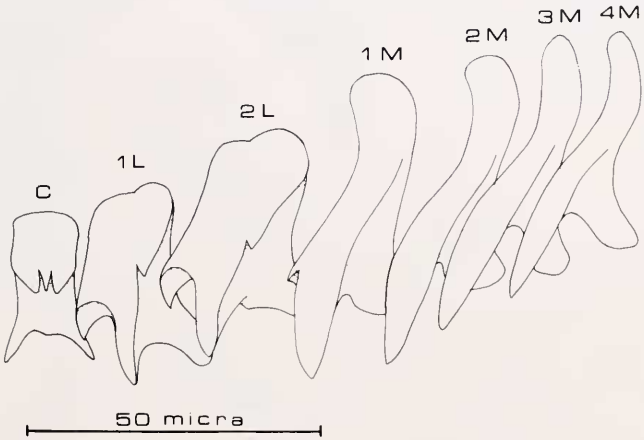

Plate 32

Radula of *Oxychilus agostinhoi*. C, central; 1L - 2L, first and second laterals; 1M - 4M, first to fourth marginals.

they receive one branch; the upper glands are round, half the length of the lower ones and free posteriorly and laterally.

Reproductive system (Plate 34, figs. 1-4): Typical of the family. Combined penis and flagellum varying from 3.3 to 5.6 mm in

Plate 31

Figs. 1-6. Radula and jaws of *Oxychilus agostinhoi*. Figs. 1-3, radula of paratype MCZ 288927 (scales = 25 μm); Fig. 4, mandible of paratype 502 (scale = 100 μm); Fig. 5, umbilical region of shell of paratype 508 (scale = 17 μm); Fig. 6, microsculpture of the third whorl of shell of paratype 501 (scale = 100 μm). C, central tooth; 1L - 2L, first and second laterals; 1M - M, first and remaining marginals.


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dgli
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dglc
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ot
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rs
pt
atn
cmn
hd
vg
vd
on
ptc
pns
art
pe
ep
cplc
mln

length; penis thick, twisted posteriorly and with a medial constriction; proximal portion wrapped in a membranous sheath, the external reflection of a strong muscular sheath (fig. 2) which does not cover the constriction; flagellum thick, short; epiphallus thinner than flagellum, shorter than total length of penis and expanding rapidly from the vas deferens; internal wall of penis and epiphallus (fig. 2) with 4 to 5 longitudinal folds, stronger in penis; penis retrac-

Plate 33

Dorsal view of dissected *Oxychilus agostinhoi;* the top of the neck was cut longitudinally and the skin reflected; a lateral cut was made on the body whorl from below the pneumostome to the top of the visceral mass, and the rectum, kidney and all the roof of mantle cavity reflected to the left; the floor of the mantle cavity was removed and most of the organs loosely separated; ovotestis and salivary glands are displaced.

acr, anterior crop
ak, anterior lobe of kidney
alb, albumen gland
art, artery
at, anterior tentacle
atn, anterior tentacle nerve
aur, auricle
bb, buccal bulb
bg, buccal ganglia
cbc, cerebro-buccal connective
cg, cerebral ganglia
cm, columellar muscle
cmn, columellar muscle nerve
dgl, digestive gland
dglc, digestive gland collector ducts
dgle, digestive gland excretor ducts
dgli, digestive gland intestinal duct
ectn, external circumtentacular nerve
eln, external lip nerves
ep, epiphallus
hd, hermaphroditic duct
i, intestine
ictn, internal circumtentacular nerve
iln, internal lip nerve
kd, kidney duct
mb, mantle border
mln, median lip nerve
ns, neck skin
oe, oesophagus
on, ocular nerve
ot, ovotestis
pc, pericardium
pcr, posterior crop
pe, penis
per, penis retractor
pk, posterior lobe of kidney
pn, pneumostome
pns, skin close to the pneumostome where *prn 1* and *vn 1* attach
prg, parietal ganglion
prn 1, first parietal ganglion
pt, posterior tentacle
ptc, posterior tentacle contractor
ptr, posterior tentacle retractor
r, rectum
rl, roof of the lung
rm, radular muscle
rs, radular sac
s, stomach
sd, salivary ducts
sgl, salivary glands
sov, spermoviduct
sp, spermatheca
spd, spermathecal duct
sv, seminal vesicle
va, vagina
vd, vas deferens
vg, visceral ganglion
vn 1, first visceral nerve
vt, ventricle

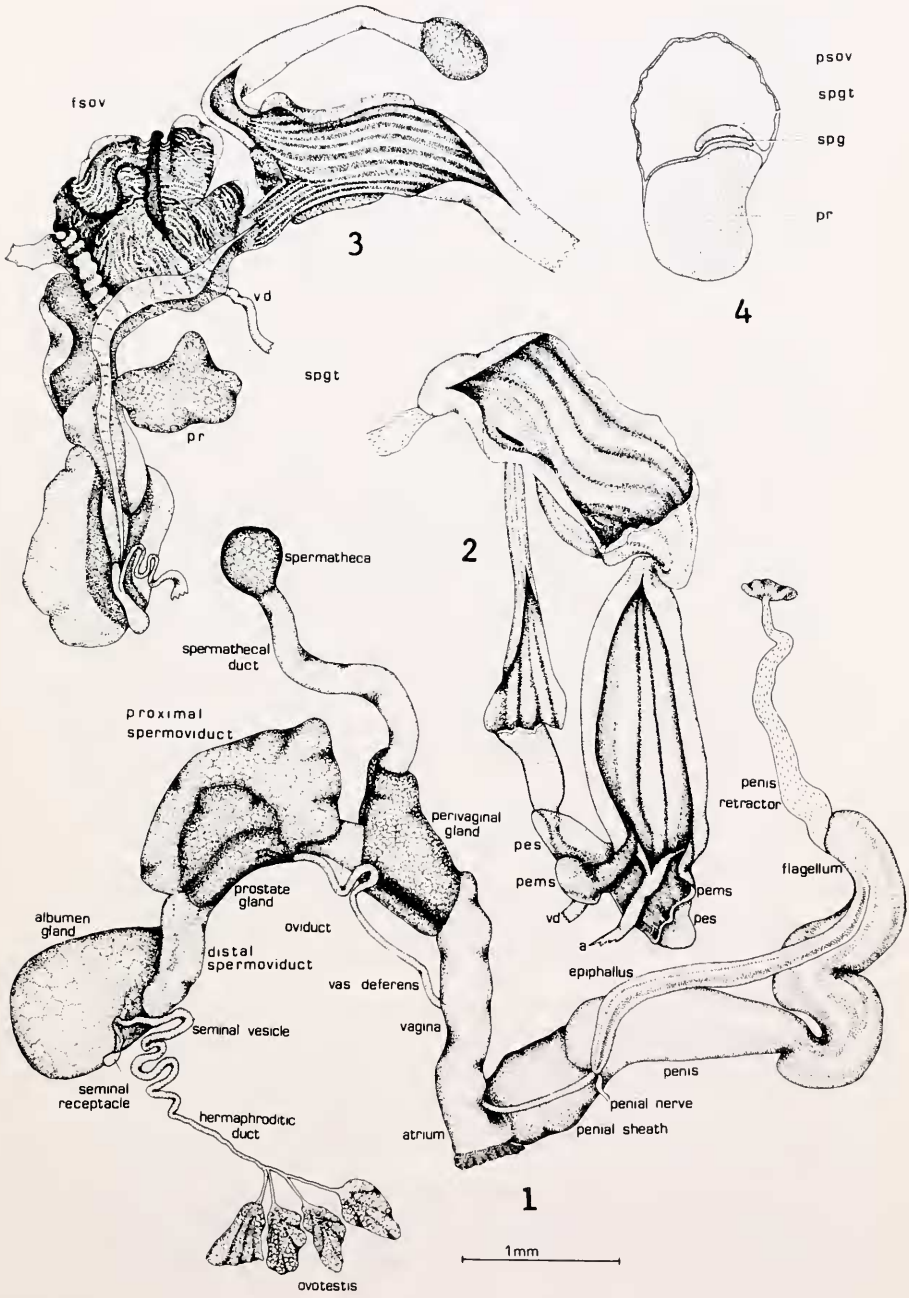
tor thick, usually short, arising from the floor of the lung posteriorly and inserting on the flagellum subapically. Genital atrium very reduced. Vagina almost as thick as penis and, together with oviduct, usually half total length of penis. Perivaginal gland thick, slightly pigmented, enveloping distal portion of vagina and proximal portion of oviduct, as well as proximal end of spermathecal duct. Spermathecal duct as thick as oviduct and as long as vagina; spermatheca pinkish, slightly elongated, twice the diameter of the spermathecal duct. Oviduct short. Internal wall of vagina and oviduct, as well as that portion of spermathecal duct covered by perivaginal gland, and with numerous longitudinal folds (Plate 34, fig. 3). Spermoviduct divided into two parts: 1. distal portion, enveloped by mucous gland, as thick as vagina; 2. proximal portion, thin walled and convoluted; the internal wall of anterior half with numerous folds, posterior half smooth (fig. 3); floor of spermoviduct covered by a thick, whitish sperm groove tract, which tapers and disappears when entering oviduct (Plate 34, figs. 3-4). Prostate gland adhering to floor and right side of proximal spermoviduct, pinkish, large, somewhat quadrangular. Albumen gland about same size as proximal spermoviduct. Ovotestis yellowish, composed of four oval lobes, the narrower ends of the lobes connecting with the hermaphroditic duct through moderately short and thin ducts, fused halfway in the first two lobes.

Digestive system (Plate 33). Buccal bulb well developed, cylindrical. Mandible (Plate 31, fig. 4) oxygnathe, semilunar in shape, strong, smooth, with a slightly curved median prominence on its free edge. Salivary glands white, well developed, fused together, forming a somewhat cylindrical mass, lying on top of the crop fitting up against the penis, spermoviduct and albumen gland. Oesophagus imperceptibly merging with the crop, which ends as a thin

Plate 34

Figs. 1–4. Reproductive system of *Oxychilus agostinhoi*. Fig. 1, external morphology; Fig. 2, internal morphology of male ducts; Fig. 3, internal morphology of female ducts; Fig. 4, diagramatic cross section of proximal spermoviduct, based on dissections and the literature.

a, atrium
fsov, folded portion of spermoviduct
pems, penial muscular sheath
pes, penial sheath
pr, prostrate gland
psov, proximal spermoviduct
spg, sperm groove
spgt, sperm groove tract
vd, vas deferens


fsov
3
vd
spgt
pr
psov
spgt
spg
pr
4
2
spermatheca
spermathecal duct
proximal spermoviduct
perivaginal gland
prostate gland
albumen gland
oviduct
distal spermoviduct
vas deferens
seminal vesicle
vagina
seminal receptacle
hermaphroditic duct
atrium
ovotestis
pes
pems
vd
a
penis retractor
flagellum
epiphallus
penis
penial nerve
penial sheath
1
1mm

walled sac. Stomach small, muscular, tapering abruptly posteriorly. Intestine short, convoluted, imperceptibly merging into the non-convoluted and slightly enlarged rectum. Digestive gland dark, its two main collector ducts merge before reaching the stomach, then subdivide into four excretory ducts, two of which empty into the anterior portion of the crop, one into the posterior portion of the crop and the other one into the stomach; an independent smaller duct empties into the anterior portion of the intestine.

Kidney (Plate 33). Bilobed, yellowish, strongly folded internally; the anterior lobe largest, on the roof of the mantle cavity, posterior to the heart; posterior lobe in visceral mass; nephridial duct S-shaped, large, arising from the tip of the anterior lobe close to the auricle, contouring its right edge and then turning forward to follow the left of the rectum, to open at the pneumostome.

Nervous system (Plate 35). Typical of the family (zonitoid type). Cerebral ganglia well developed, separated by very short cerebral commissure, with 21 nerves emerging from the ganglia, six of them connectives. The single unpaired penial nerve emerges posterior to the right external circumtentacular nerve and enters the penis where the penial sheath adheres to the epiphallus. There are seven sets of paired nerves emerging from the cerebral ganglia:

1. Internal circumtentacular nerves emerge from the front portion of the ganglia, close to the cerebral commissure, and attach to the basal wall of the posterior tentacle.
2. External circumtentacular nerves arise at the latero-posterior side of the ganglia and insert on the external basal wall of the posterior tentacle.
3. Ocular nerves are very thick, arise lateral to the internal circumtentacular nerves, insert on the proximal portion of the posterior tentacle, and continue inside it up to the eye, where they enlarge.
4. External lip nerves arise anterior to the external circumtentacular nerves on the lower surface of the ganglia and insert on the sides of the upper lip.
5. Internal lip nerves originate internal to the median lip nerves and insert internally below the base of the anterior tentacles.
6. Median lip nerves are thick, originate anterior to the previous ones, and extend to the anterior tentacle muscles. At the proximal end of the anterior tentacle muscle the median

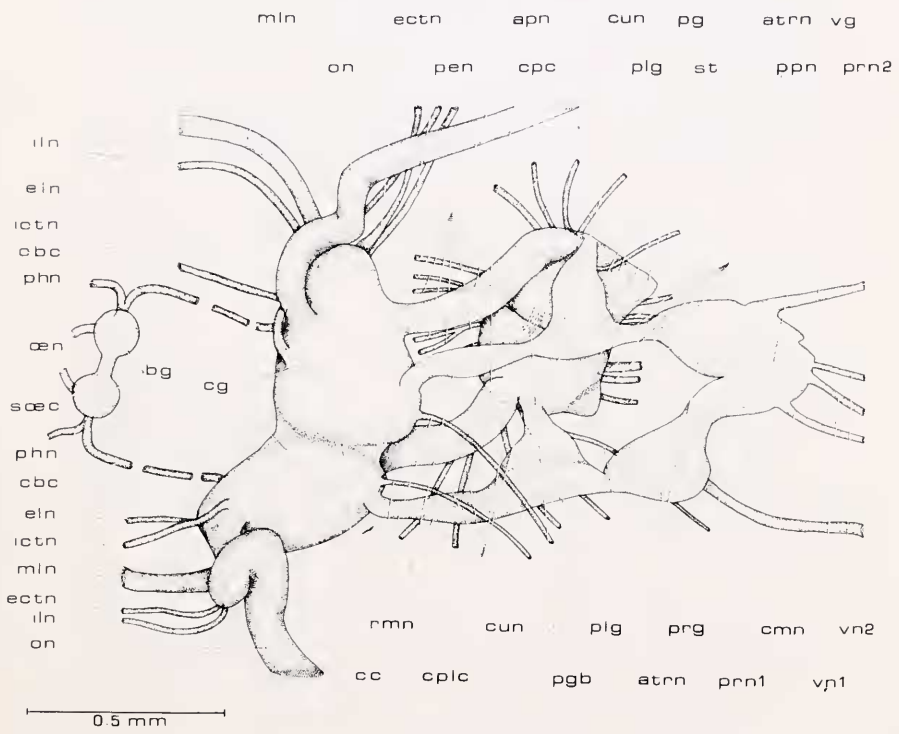


Plate 35

Dorsal view of central nervous system of *Oxychilus agostinhoi*.

apn, anterior pedal nerves
atrn, anterior tentacle retractor nerve
bg, buccal ganglia
cbc, cerebro-buccal connectives
cc, cerebral commissure
cg, cerebral ganglia
cmn, columellar muscle nerve
cpc, cerebro-pedal connectives
cplc, cerebro-pleural connectives
cun, cutaneous nerves
ectn, external circumtentacular nerve
eln, external lip nerve
ictn, internal circumtentacular nerve
iln, internal lip nerve
mln, median lip nerve
oen, oesophagial nerves
on, ocular nerve
pen, penial nerve
pg, pedal ganglia
pgb, pedal ganglia bridge
phn, pharyngeal nerves
plg, pleural ganglia
ppn, posterior pedal nerves
prg, parietal ganglia
prn 1 - prn 2, parietal nerves
rmn, radular muscle nerves
soec, suboesophagian commissure
st, statocyst
vg, visceral ganglion
vn 1 - vn 2, visceral nerves

lip nerve gives rise to a short anterior tentacle nerve, then divides: one branch has three fusiform thickenings and the other one two; they insert on the base of the anterior tentacles.

7. Radular muscle nerves emerge from the posterior end of the ganglia; the left one loops above and around the left salivary duct; the right nerve curves below the oesophagus.

The right internal circumtentacular, the right ocular and the right external circumtentacular cross the reproductive organs in between the penis and the vagina.

Connectives leaving the cerebral ganglia:

1. Cerebro-buccal connectives, very long, emerge from below the front side of the ganglia and extend to the buccal ganglia, which are located below the proximal end of the oesophagus between the proximal ends of the salivary ducts. The oesophageal nerves emerge from the buccal ganglia, and the pharyngeal nerves from the point of insertion of the cerebro-buccal connectives.

2. Cerebro-pedal connectives, short and thick, emerge from the posterior end of the cerebral ganglia and connect laterally with the pedal ganglia.

3. Cerebro-pleural connectives, short and thick, emerge internal to the previous ones.

Pleural ganglia elongate, twice the diameter of the connectives; bridges to the parietal ganglia very short, tapering downward to the pedal ganglia, and assuming the shape of a triangle; they are about the same size as the other connectives at the point of insertion with the pedal ganglia; at the point of the insertion of the pleuro-pedal connectives emerge the anterior tentacle retractor nerves. The parietal ganglia are asymmetrical; left parietal about the same size as the pleural ganglia, connects to the visceral ganglion through a broad and short connective; from the latero-posterior portion of the left parietal ganglion emerges a parietal nerve, which inserts on the neck, close to the floor of the lung; right parietal larger than the left one, fused with the visceral ganglion, but distinguishable from this one by its outline; it bears also one nerve, which emerges latero-posteriorly and attaches near the pneumostome region. Visceral ganglion about the same size as the right parietal, bears three nerves: the one on the left emerges latero-

posteriorly and inserts into the columellar muscle, the one in the middle disappears into the albumen gland after passing close to the tip of the ventricle, and the one on the right inserts on the lung, in the proximity of the pneumostome. Pedal ganglia broad, circular, somewhat flattened, separated by a commissure similar to the one in the cerebral ganglia, connected dorsally by a bridge of fibrous appearance. They give rise to 18 nerves:

1. Three short pairs emerge posteriorly and sink immediately into the foot.
2. Four pairs (cutaneous) emerge laterally and go to the skin of the neck; both middle right cutaneous cross the genital organs.
3. Two pairs emerge anteriorly; the outside pair continues to the side of the anterior portion of the neck, and the inside pair subdivides into two branches: the outer branch goes to the anterior tip of the foot and the inner branch attaches to the outer edge of the lower mucous glands.

Remarks

According to Riedel (1964) the groups of the genus *Oxychilus* Fitzinger endemic to the Azores are derived from a pre-*Ortizius* type of snail which came to the Azores from Europe sometime during the Tertiary. It gave rise to:

1. The subgenus *Ortizius* Forcart with three species: *O. (O.) miguelinus* (L. Pfeiffer), *O. (O.) juvenostriatus* Riedel and *O. (O.) ornatus* Riedel.
2. The subgenus *Radiolus* Wollaston, with only one species, *O. (R.) volutella* (L. Pfeiffer).
3. The subgenus *Drouetia* Gude, with until now, a single polytypic species, *O. (D.) atlanticus* s.l., which includes at least three subspecies: *O. (D.) atlanticus atlanticus* (Morelet and Drouet), *O. (D.) atlanticus minor* (Morelet) and *O. (D.) atlanticus brincki* Riedel.
4. The subgenus *Atlantoxychilus* Riedel, with one species, *O. (A.) spectabilis* (Morelet), which arose from the subgenus *Drouetia* Gude.

Reported from Santa Maria are: *Oxychilus (O.) miguelinus*, *O. (R.) volutella*, *O. (D.) atlanticus brincki* and *O. (A.) spectabilis*.

Table 2. Comparative table of the characteristics of the Azorean species of the subgenera *Ortizius* Forcart, *Drouetia* Gude and *Atlantoxychilus* Riedel, and of *Oxychilus (Drouetia) agnostinhoi* n. sp. Partly based on data from Riedel (1964).

	SHELL							RADULA			REPRODUCTIVE ORGANS		
TAXONOMIC UNIT	MD	W	SP	AP	U	COL	MIC	T/R	R	CC	PE (ext.)	PE (int.)	PVG
ORTIZIUS	5.5 to 15.0	4¼ to 5¾	somewhat raised	depressed and oblique	yes	transparent to translucent; dark-light radial bands moderately compact	fine to marked	31 to 39	34 to 46	longer than laterals	constriction always covered by penial sheath	weak longitudinal folds; sometimes transverse furrows also present	well developed; darkly pigmented
DROUETIA	7.0 to 9.0	5 to 6	raised to somewhat raised	raised and somewhat oblique	no	fairly transparent uniform	very fine	41 to 46	54 to 58	longer than laterals	no constriction	strong longitudinal folds	weakly to well developed; slightly pigmented
ATLANTOXYCHILUS	5.5	5	raised	raised and somewhat oblique	no	fairly transrent; dark-light radial bands somewhatcompact	very fine and very weak; deep spiral furrow	41	46	longer than laterals	no constriction	strong longitudinal folds and papillae	weakly developed. slightly pigmented
OXYCHILUS (D.) AGOSTINHOI	5.1	4¼	very flat	depressed and oblique	no	transparent to translucent; unevenly spaced dark-light radial bands	weak and very fine	29 to 31	42 to 55	same size as laterals	constriction always above penial sheath	strong longitudinal folds	well developed; slightly pigmented

AP – aperture
CC – central cusp of central tooth
COL – external appearance and coloration
MD – maximum diameter in mm
MIC – microsculpture
PE (ext) – external morphology of penis
PE (int) – internal morphology of penis
PVG – perivaginal gland
R – number of rows of teeth
SP – spire
T/R – number of teeth per row
U – umbilicus
W – number of whorls

Despite a thorough search of Santa Maria, I failed to collect the first two species. *Oxychilus (D.) atlanticus brincki* is considered endemic to Santa Maria; however, some specimens I collected on Terceira Island are very similar to this subspecies although they possess a much longer epiphallus. Anatomical studies are needed in both groups to determine whether or not they are consubspecific.

Oxychilus (D.) agostinhoi shares characteristics with species of the subgenus *Ortizius* as well as of the subgenera *Drouetia* and *Atlantoxychilus*. This can be easily seen in Table 2. Other characteristics of the new species, not included in Table 2 due to lack of comparative data are:

1. The fine spiral lines on the shell are crossed by finer more compact axial lines, more easily visible in less transparent specimens. This pattern is stronger in *O. (D.) atlanticus brincki*, and weaker in *O. (A.) spectabilis*.
2. The absence of large light-dark patches in the mantle which are visible through the shell of *O. (A.) spectabilis* and all subspecies of *O. (D.) atlanticus*.
3. The grayish to white foot of *O. (D.) agostinhoi* relates it to species of *Ortizius*; the foot of *Drouetia* group is usually deeply colored, yellow to brilliant orange.
4. The mandible is identical to that of *O. (D.) atlanticus brincki*, but very different from the narrow, fragile mandible of *O. (A.) spectabilis*. Lack of material does not permit a comparison with other subspecies of *O. (D.) atlanticus* or with the endemic species of *Ortizius*.

In spite of these differences, I feel that the establishment of a new subgenus is unwarranted and that, based on the shell and internal structure of the penis, this species belongs in the subgenus *Drouetia*. However, its relationship to other species of *Oxychilus* endemic to the Azores elucidates the phylogenetic position of the up-to-now monotypic, endemic subgenus *Drouetia*. Its resemblance to the recent Azorean species of the subgenus *Oritizius* supports the hypothesis of Riedel (1964). Based only on these resemblances, for there is no fossil record, I think that *Oxychilus (Drouetia) agostinhoi* probably arose from the branch leading to the *O. (D.) atlanticus* s. l. before the origin of the subgenus *Atlantoxychilus* (Plate 36).

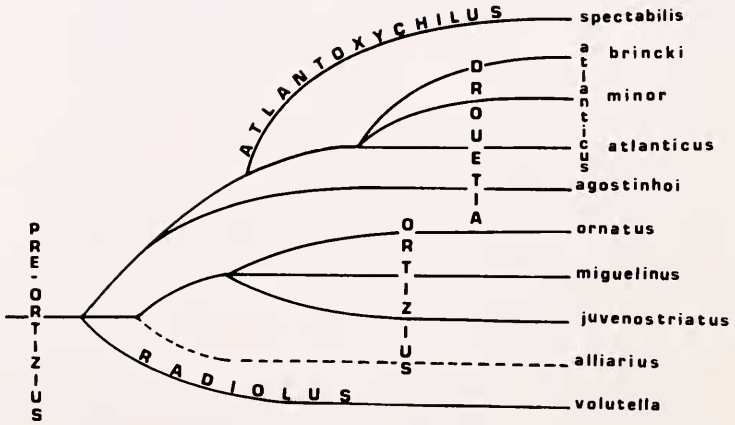


Plate 36

Diagramatic representation of the relationship of the Azorean species of *Oxychilus* Fitzinger, except for *Oxychilus s. s.* (Adapted from Riedel, 1964).

———— species and groups endemic to the Azores

— — — — — species living also in Europe

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MISCELLANY

STANLEY TRUMAN BROOKS, A BIBLIOGRAPHY OF HIS WORK ON MOLLUSKS WITH A CATALOGUE OF HIS MOLLUSCAN TAXA.

RICHARD I. JOHNSON

Stanley Truman Brooks was born on October 4, 1902 in Mound City, Kansas. He attended the University of Kansas where he received an A.B. degree in 1926. He did graduate work at the University of Pittsburgh, receiving a M. S. in 1927 and a Ph. D. in 1929. Between 1926 and 1928 he was an assistant in the Department of Invertebrate Zoology, then under the direction of Arnold E. Ortmann (Johnson, 1977). Most of his work was on North American land and fresh water mollusks. After Ortmann's death in 1927, Brooks was appointed curator of the department, a post he held until 1946. He then took a year's leave of absence to act as a scientific specialist for the United States Military Government in Germany. He never returned to the Museum, but for the rest of his life worked for a tobacco company. Brooks died of emphysema in 1960 (pers. comm., J. J. Parodiz).

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MOLLUSCAN TAXA INTRODUCED BY S. T. BROOKS

ABBREVIATIONS

CM – Carnegie Museum, Pittsburgh, Pennsylvania

MCZ – Museum of Comparative Zoology, Cambridge, Massachusetts

clappi Brooks and Hunt, *Vertigo*

1936, Ann. Carnegie Mus. *26:* 121, fig. 1 (Renick, Greenbrier Co., West Virginia). Holotype CM 62.28186.

mariae Brooks, *Plectostylus*

1936. Ann. Carnegie Mus. *25:* 124 and figure (San Esteban, Chile). Holotype CM 62.28184.

newfoundlandensis Baker and Brooks, *Stagnicola*

1935, Nautilus *49:* 12 (Camp 31, 8 mi. from Lomond, Bonne Bay, Newfoundland). Measured holotype CM 62.26763; paratype MCZ 108814.

papyracea Baker and Brooks, *Stagnicola palustris*

1935, Nautilus *49:* 10 (Rocky Pond near Whitbourne, Newfoundland). Measured holotype CM 62.26761; paratype MCZ 108813.

perpalustris Baker and Brooks, *Stagnicola palustris*

1935, Nautilus *49:* 11 (Pools along Exploits River, Grand Falls, Newfoundland). Measured holotype CM 62.26762; paratype MCZ 108812.

pilsbryi Brooks, *Aplexa hypnorum*

1935, Nautilus *48:* 100 (Pond near White Rocks River, at Paradise Creek, White Rocks Canyon, Uinta Co., Utah, Twp. 2 S, Range 18 E, Salt Lake Meridian). Holotype CM 62.26773. Figured by Brooks, 1936, Nautilus *50:* 14, fig. 1.

platysayoides Brooks, *Polygyra.*

1932, Nautilus *46:* 54–55, 3 text figs. (Cooper's Rock, Monongahela Co., West Virginia). Holotype CM 62.23750.

praelonga Brooks and MacMillan, *Pomatiopsis*

1940, Nautilus *53:* 96, pl. 12, fig. 2 (Hillside along Elk River, 1.5 mi. S Clay Co., West Virginia). Holotype CM 62.32897.

rugosa Brooks and MacMillan, *Triodopsis tridentata*

1940, Nautilus *53:* 96, pl. 12, fig. 3 (Damp Ravine, Blair Mountain, 1 mi. SW Blair, Logan Co., West Virginia). Holotype CM 62.32899.

sanctivincentii Brooks, *Natica*

1933, Ann. Carnegie Mus. *21:* 413, fig. 1 (West Coast of St. Vincent, British West Indies). Syntypes CM 62.3369.

vagabondiae Brooks, *Plectostylus*

1936, Ann. Carnegie Mus. *25:*125 and figure (San Esteban, Chile). Holotype CM 62.28185.

uinta Brooks, *Oreohelix eurekensis*

1939, Nautilus *52:* 105 (Hominy Creek, R. 1 W., T. 3., 3 mi N Uinta Special Meridian, near Whiterocks, Uinta Co., Utah). Measured holotype CM no. [not given, and now apparently lost (pers. comm., J. J. Tripp)]. Paratype Acad. Nat. Sci. Philadelphia, fig. by Pilsbry, 1939, Acad. Nat. Sci. Philadelphia, Monograph 3, 1 (1): 534, fig. 348, lower figs.